



Vegetation distribution along mountain environmental gradient predicts shifts in plant community response to climate change in alpine meadow on the Tibetan Plateau

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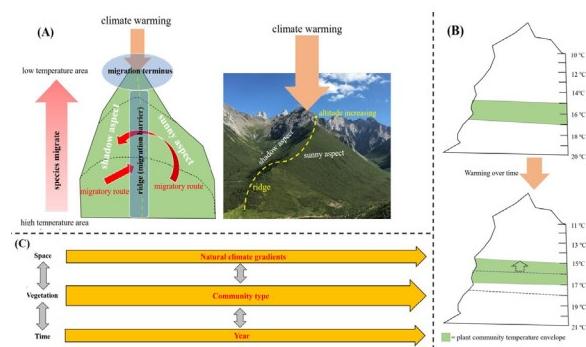
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HIGHLIGHTS

- Using “space-for-time substitution” to study plant responses to climate warming
- Plant diversity significantly decreases with climate warming.
- Community biomass remains unchanged with climate warming.
- The change of community species composition is more dependent on the migratory ability of broadleaf forbs.

GRAPHICAL ABSTRACT



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ABSTRACT

Plants are particularly sensitive to climate change in alpine ecosystem of the Tibetan Plateau. The various mountain micro-climates provide a natural gradient for space-for-time substitution research that plant responses to climate change. In this study, we surveyed the plant community in term of species composition, diversity and biomass across 189 sites on a hill of the Tibetan Plateau and analysed the individual and integrated effects of soil temperature and moisture on the plant community. The results showed that, at the quadrat scale, there were decrease in richness of 1.08 species for every 1 °C increase in soil temperature and 3.56 species for every 10% decrease in soil moisture. The integrated effects of increasing soil temperature and decreasing moisture are expected to lead to a rapid decrease in species richness. Biomass had no significant correlation with soil temperature but significantly decreased with soil moisture decreasing ($p < 0.01$). Biomass would decrease when soil moisture was below 20%, no matter how the change of soil temperature. We also found that gramineae and perennial forbs were sensitive to climate change. With soil temperature increased, the proportion of gramineae increased, whereas the proportion of perennial forbs decreased. The integrated effects of soil temperature increasing and moisture decreasing caused a shift from sedge-controlled to gramineae-controlled communities in alpine meadow. This study not only enhances our understanding of mountain plant community dynamics under climate change, but also predicts the shift of vegetation response to climate change on high-elevation alpine meadow.

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1. Introduction

Global climate change is one of the most serious challenges facing humanity (IPCC, 2007; Seddon et al., 2016). The average global temperature has increased by 0.065 °C per decade since 1880, accompanied by significant changes in precipitation patterns (Ma et al., 2017). These rapid climate changes, unprecedented in human history, are likely to profoundly affect the functioning of terrestrial ecosystems (Garcia et al., 2014; Seddon et al., 2016). Climate change has been demonstrated to influence community structure and species interactions, which could potentially translate into changes in community biomass production, species diversity and species composition (Yang et al., 2011; Baldwin et al., 2014; Rudgers et al., 2014). Predicting and understanding the quantitative effects of global change on plant communities remains a key challenge, especially for the regions where long-term ecological data is scarce (Lester et al., 2014).

The Tibetan Plateau, the largest and highest plateau in the world, is known as the “third pole” of the Earth, and it is highly sensitive to climate change (Liu et al., 2018). Because, the current species composition in alpine region is the result of on-going speciation processes by adapting climate. High altitude restricted species are also the most threatened due to the limited areas into which they can migrate under conditions of increasing temperatures (Madriñán et al., 2013). Over the past six decades, the rate of climate warming on the Tibetan Plateau has been more than twice the global average (Chen et al., 2013; Ma et al., 2017), along with changes in precipitation patterns (Shen et al., 2015). The alpine meadow is the main ecosystem type on the Tibetan Plateau. Climate change is an important topic in ecological research in the sensitive alpine meadow ecosystem of the Tibetan Plateau. Both natural climate gradient studies and experimental climate manipulations have been performed to quantify effects of climate change on alpine ecosystems (Chen et al., 2013). Dunne et al. (2004) also integrated experimental/gradient research to study climate-ecosystem interaction. There are a few historical data in the long-term manipulation studies, accompanied by equally long-term field vegetation censusing to study the response of vegetation under climate change on the Tibetan Plateau (Chen et al., 2013; Ma et al., 2017; Liu et al., 2018). Short-term climate manipulation experiments in filed have frequently been used to simulate the effects of climate change on plant composition, species diversity, biomass, biochemical cycle and litter decomposition of plant communities in the alpine meadow in this region (Chen et al., 2013; Shi et al., 2014; Shen et al., 2015; Liu et al., 2018). Some studies have indicated that plant community biomass and species diversity show variable responses, involving decreases, increases, or no change, to climate change in arctic and alpine regions (Klein et al., 2007; Post and Pedersen, 2008; Wang et al., 2012). Notably, the effects of climate warming and altered precipitation on plant community properties, including plant composition, species diversity, biomass, and succession direction, may not be independent of each other. However, initial community responses to experimental climate change may greatly differ from the responses observed when the manipulation is sustained over longer periods (Dunne et al., 2004; Harte et al., 2015). There is not enough time for plants to adjust and adapt in the short experimental period, as a result, making it difficult to truly reflect the long-term responses of plants to climate change (Travis and Hester, 2005; Lester et al., 2014).

Within some studies, soil temperature and moisture gradients have been mainly used to describe climate change, whether focusing on natural climate gradients or climate manipulations (Shi et al., 2014; Harte et al., 2015; Little et al., 2016; Ma et al., 2017; Panetta et al., 2018). Space-for-time substitutions, also known as ergodic gradient studies, are often used to develop quantitative predictions of ecological responses to climate change (Travis and Hester, 2005; Lester et al., 2014). Natural gradient studies have been applied to a wide range of ecological variables in the past, often with great success (Dunne et al., 2004; Travis and Hester, 2005; Lester et al., 2014). The Tibetan Plateau is a large mountain system consisting of contiguous mountains and

hills and the long-term ecological data is scarce. The vegetation in plateau mountains is compressed into a smaller spatial scale. The mountain slope and altitude create a distinct gradient of the soil temperature and moisture, which provide the gradient studies of plant responses global climate change using space-for-time substitution (Cortés and Wheeler, 2018). The distribution of vegetation along a temperature and moisture gradient under natural conditions is the result of plant adjustment and adaption to the micro-climate over a very long period of time, therefore, it can truly reflect the long-term adaptation of plants to the climate. Thus, space-for-time substitutions use multiple sites across a mountain environmental gradient to predict a temporal trajectory in ecological change that is assumed to be causally related to changes across the gradient (Dunne et al., 2004).

In our study, we selected a representative alpine meadow on a hill located in the north-eastern Tibetan Plateau and studied the changes in plant community along temperature and moisture gradients at the hill scale over several hundred hectares. The value of predictions from gradient analyses at hill scale depends on the fact that the plant community will track the changing climate over time in the same way that the plant community now varies with microclimate variability over space (Dunne et al., 2004; Travis and Hester, 2005). Although we adopt the space-for-time assumption in this work, we are aware that the time scales for establishment of vegetation patterns along spatial gradients may be much longer than the time scale governing vegetation responses to anthropogenic global warming. Blois et al. (2013) also concluded that predictions relying on space-for-time substitution were ~72% as accurate as “time-for-time” predictions. The largest soil temperature difference in the surface layer (0–30 cm) on the hill was around 10 °C. The Tibetan Plateau has experienced more rapid climate warming with 0.2 °C per decade over the past 50 years (Chen et al., 2013; Ma et al., 2017). Likewise, in the past 65 years (1951–2016), there has also been an average temperature increase of 0.23 °C per decade in this study area. Therefore, it takes approximately 500 years to increase the average temperature by 10 °C. The trend of changes in the species composition, diversity and biomass of the alpine meadow community were quantitatively predicted under the individual and integrated effects of soil temperature and moisture in this study. Besides, the possible succession directions of the community under climate change were predicted. Our purpose was to understand how climate change would affect the changes in alpine meadow plant community and the potential adaptive mechanisms of the plant community to climate change on the Tibetan Plateau.

2. Materials and methods

2.1. Study area

The study area is located on the north-eastern Tibetan Plateau ($37^{\circ}09'–37^{\circ}14' \text{N}$, $102^{\circ}40'–102^{\circ}47' \text{E}$). It is part of the Qilian Mountain in Tianzhu Tibetan Autonomous County in Gansu Province, China. Based on a systematic survey of mountain vegetation and topography in the study area, we selected the pasture of an alpine meadow on a hill with an altitude of 2850–3200 m (Fig. 1A). It is a winter grazing pasture and the pasture area is 150 hm^2 . The length from the bottom to the summit of the mountain along the ridgeline is 3.2 km. In the past 65 years (1951–2016), there has been an average annual temperature increase of 0.23 °C per decade in this area, but no trend of significant changes was observed in the average annual precipitation during the past 65 years (Fig. 1B). This area is an ideal place to study the effects of climate change on vegetation. For the past 5 years, the average annual temperature was 0.83 °C, and the cumulative temperature of growing degree days (GDD; sum of daily mean temperatures above 5 °C) were 1097 °C. The average annual precipitation was 463 mm and was mainly concentrated in July–September, accounting for 76% of the total annual precipitation. The annual potential evaporation was 1592 mm. The mountain is also part of the seasonal snowfall region, and all the snow melts within a few days. The plant growth period lasted 120–140 d.

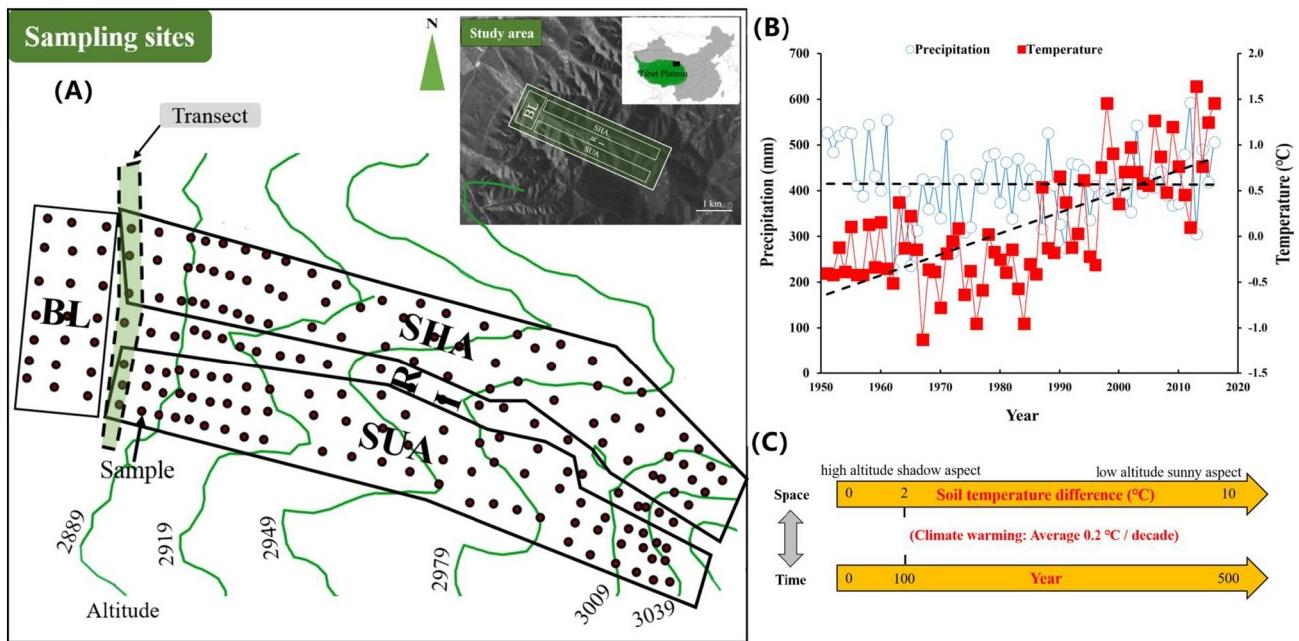


Fig. 1. A: Location of the study area on the Tibetan Plateau and the sampling points within a hill. (BL: bottomland; SHA: shadow aspect; RI: ridge; SUA: sunny aspect). B: Temperature and precipitation changes during 1951–2016. C: Conceptual depiction of space-for-time substitution.

The soil type was alpine meadow soil, and there was a significant positive correlation between soil temperature and air temperature. The grassland type in the study area was typical alpine meadow.

2.2. Experimental and sampling design

The study area of the hill was divided into four sites: bottomland (BL), shady aspect (SHA), ridge (RI) and sunny aspect (SUA Fig. 1A). A total of 27 transects (including the shady aspect, ridge and sunny aspect) along the ridgeline at 5 m vertical intervals of altitude from the bottomland (2850) to the summit (3020 m) were established. In these transects, there were 189 sampling sites. Plant community structure and composition, soil temperature and moisture and environmental variables were surveyed in the sites. Based on the temperature differences of around 10 °C between the low-altitude sunny aspect and high-altitude shadow aspect within the same hill and the average warming 0.2 °C per decade, we simulated and predicted the quantitative effects of climate change on the plant community of the alpine meadow on the Tibetan plateau for next 500 years (Fig. 1C).

2.3. Plant survey and soil temperature and moisture measurements

A plant community survey was conducted in August (the peak of growing season). The plant communities were surveyed along an altitude gradient in the bottom land and different slope aspects of the hill. The number of species present within a 0.5 m × 0.5 m quadrat was recorded as the species richness; the number of each plant species in the quadrat was recorded as the species abundance, and the plants were dried in an oven at 75 °C to obtain the above-ground biomass of each species. In each quadrat, the coverage of each species was recorded. In addition, the height of each plant species was recorded. Sampling circles were thrown at random 20 times around each quadrat for frequency measurement. The relative abundance, biomass, coverage, height, and frequency of species were calculated using the maximum normalization method. The importance values of species were expressed as the means of the relative abundance, biomass, coverage, height and frequency of species in the community. The species evenness and Berger-Parker indices of the community in each quadrat were calculated (Magurran, 1988).

At each site, the temperature and moisture in the 0–10, 10–20 and 20–30 cm soil layers were measured using a TZS-IIW soil water and temperature measuring device (Zhejiang Top Instrument Co., Ltd., Hangzhou, China). Five measurements were made, and the means were taken as the soil temperature and moisture for the site. The latitude, longitude and altitude of each site were recorded using a Garmin handheld GPS.

2.4. Data processing

Multiple comparisons were made for species richness, abundance, evenness, Berger-Parker dominance, biomass, soil temperature and moisture between sites in different slope aspects using the least significant difference (LSD) method. The relationships of soil temperature and moisture with species diversity (richness, abundance, evenness and Berger-Parker dominance) and biomass were analysed by partial correlation analysis. To eliminate the mutual interference between soil temperature and moisture, which could affect their respective relationships with species diversity and biomass. The species were classified into four functional groups (gramineae, sedge, perennial forb and annual forb).

Multivariate ordination was performed to comprehensively explain the changes in soil temperature and moisture versus the changes in plant community species composition and to predict the possible succession direction of the community in relation to increases in soil temperature and changes in soil moisture. Plant data were represented by matrices of four quantitative features: species coverage, abundance, richness [the presence and absence of each species in the sites, denoted as (0, 1)] and biomass of plant communities, with 189 sites for each quantitative feature. Soil temperature and moisture data were matrices of soil temperature and moisture in the 0–30 cm soil layer. CCA was performed for a comprehensive analysis of plant species distribution in terms of four quantitative features (coverage, abundance, richness and biomass) at the family and species levels of the community, and the relationships of these features with changes in soil temperature and moisture factors were analysed. In the species-level ordination, the distribution ranges of different functional groups were marked to indicate their potential habitat. Additionally, two-dimensional ordination diagrams were drawn by a T-value test for the effects of soil temperature and moisture on the community at the family level (Šmilauer and Lepš, 2014).

Table 1
The distribution of plant species diversity and biomass production as well as dominant species induced by micro-climate features of different hill aspects on a hill in north-eastern Tibetan Plateau.

Plot	Altitude (m)	Family	Genera	Species	Coverage (%)	Abundance	Species richness	Biomass (g/m ²)	Evenness	Berger-Parker	Dominant species
Bottom land	2850	13	24	32	82.58 ± 8.61 ^c	154.23 ± 60.04 ^c	11.00 ± 2.66 ^c	245.82 ± 54.27 ^b	0.80 ± 0.02 ^a	0.10 ± 0.01 ^b	<i>Elymus nutans</i>
Shadow aspect	2860–3020	19	47	55	93.24 ± 3.46 ^a	356.50 ± 118.59 ^a	24.98 ± 10.25 ^a	347.64 ± 120.05 ^a	0.65 ± 0.03 ^c	0.20 ± 0.06 ^a	<i>Stipa grandis</i> <i>Poa cymophylla</i> <i>Polygonum viviparum</i> <i>Kobresia capillifolia</i> <i>Thlaspium aquilegfolium</i> <i>Kobresia capillifolia</i> <i>Artemisia smithii</i> <i>Polygonum viviparum</i> <i>Koeleria cristata</i> <i>Leymus secalinus</i>
Ridge	2860–3020	13	34	43	93.97 ± 4.91 ^a	373.42 ± 131.19 ^a	22.04 ± 3.69 ^a	373.42 ± 131.19 ^a	0.68 ± 0.07 ^c	0.18 ± 0.03 ^a	
Sunny aspect	2860–3020	18	40	48	88.17 ± 7.32 ^b	235.89 ± 121.09 ^b	18.11 ± 7.44 ^b	235.89 ± 121.09 ^b	0.73 ± 0.09 ^b	0.19 ± 0.05 ^a	

All values represent mean values (±SE). Within a given plant community characteristic, different superscripts indicate a significance among different plots, at $p < 0.05$, $n = 189$ (ANOVA followed by the least significant difference test).

Preliminary statistical analysis of the data was performed using Excel 2013 and SPSS 19.0 software. The curve of the species accumulation rate was generated using EstimateS Win910 software. The significance threshold was pre-established as $\alpha = 0.05$, and multivariate ordinations were implemented using ArcGIS 10, the SAS JMP 10.0 package and CONOCO 5.0 for Windows.

3. Results

3.1. Distribution of soil parameters and plant species diversity as well as biomass production induced by micro-climate features

There were 68 species, 54 genera, and 23 families of plants in the study area (Table 1). The variation of coverage, abundance, biomass, richness, evenness and Berger-Parker indices among different aspects was significant. Due to the long-term effects of the micro-climate, the bottom land and the sunny aspect were dominated by mesophytic and drought-tolerant gramineae, and the dominant species were *Elymus nutans* and *Koeleria cristata*, respectively; the shady aspect and the ridge were dominated by mesophytic and shade-tolerant broadleaf forbs and sedges, with the dominant species being *Polygonum viviparum* and *Kobresia capillifolia*, respectively.

3.2. Distribution pattern of soil temperature and moisture in the study area

As Fig. 2 shows, the soil temperatures at different depths in the sunny aspect were significantly higher than that in the ridge and shady aspects. The temperature difference in the surface soil (0–30 cm) between sunny aspect with highest soil temperature and shadow aspect with lowest soil temperature reached 10 °C. Soil moisture in the shady aspect was significantly higher than that in the ridge and sunny aspects. Both soil moisture and temperature, there were a trend of gradually changing from sunny aspect to shadow aspect. With altitude increased, soil temperature in the shady aspect did not change evidently, while the soil temperature in the sunny slope firstly increased and then decreased. The soil moisture of different aspects and soil depths always increased with altitude increasing.

3.3. The individual and integrated effects of soil temperature and moisture on species diversity

Species richness decreased significantly with increasing soil temperature ($R^2_{\text{partial}} = 0.218$, $P_{\text{partial}} = 0.000$), and there was a decrease in species richness of 1.0803 species with every 1 °C increase in soil temperature. Besides, species richness increased significantly with the increase in soil moisture ($R^2_{\text{partial}} = 0.272$, $P_{\text{partial}} = 0.000$), and there was an increase in species richness of 3.559 with every 10% increase in soil moisture. Species abundance had no significant correlation with soil temperature or moisture. Moreover, species evenness increased significantly with the increase in soil temperature ($R^2_{\text{partial}} = 0.297$, $P_{\text{partial}} = 0.000$), and it decreased significantly with soil moisture increasing ($R^2_{\text{partial}} = 0.344$, $P_{\text{partial}} = 0.000$). The Berger-Parker index significantly increased with soil moisture increasing ($R^2_{\text{partial}} = 0.106$, $P_{\text{partial}} = 0.002$) (Fig. 3A).

Fig. 3B show that high species richness was concentrated in areas with a soil temperature lower than 15 °C and soil moisture higher than 20%. When the soil moisture was below 20%, the species richness remained low regardless of the soil temperature. Similarly, species abundance was low when the soil moisture was <20%. However, species evenness was high when the soil moisture was below 20%, regardless of the soil temperature. Lower evenness occurred in areas with lower soil temperatures and higher soil moisture. The Berger-Parker index was low when the soil moisture was <30%, regardless of the soil temperature. Higher Berger-Parker index appeared in the area with lower soil temperature and higher moisture (Fig. 3B).

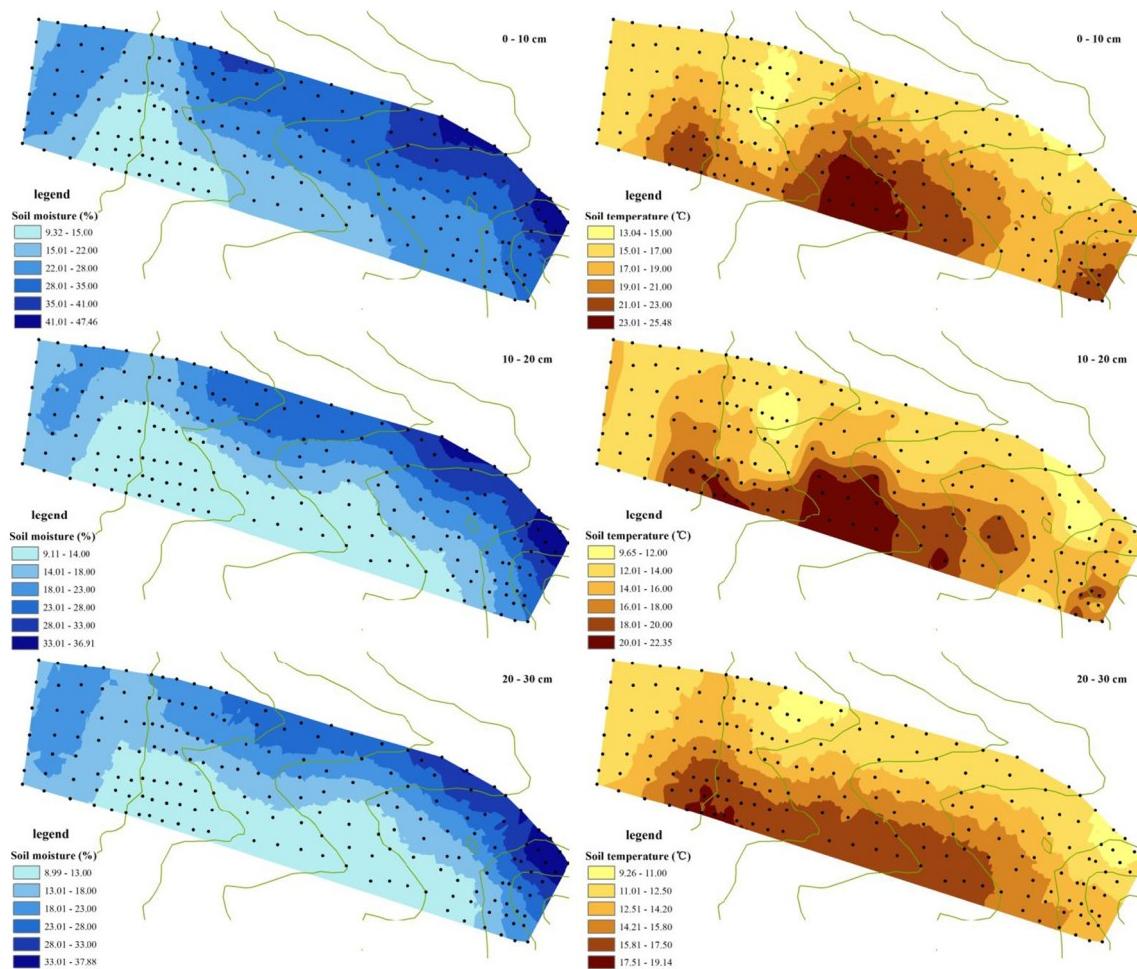


Fig. 2. Distribution pattern of soil temperature and moisture in the study area.

3.4. The individual and combined effects of soil temperature and moisture on biomass

As Fig. 4A shows, biomass had no significant correlation with soil temperature, but it significantly increased with soil moisture increasing ($R^2_{\text{partial}} = 0.056$, $P_{\text{partial}} = 0.003$). Biomass was low when soil moisture was <20%, regardless of soil temperature. The higher biomass appeared in areas with soil temperature of 12 °C and soil moisture of 30%, soil temperature of 14 °C and soil moisture of 40%, and soil temperature of 18 °C and soil moisture of 20% (Fig. 4B).

3.5. The individual and integrated effects of soil temperature and moisture on community composition and succession

The ordination results of four quantitative features (coverage, abundance, richness and biomass) of the plant community are shown in Fig. 5A. Perennial forb showed the largest number of species and the broadest range of distribution, followed by annual forb and gramineae. Sedges showed the most concentrated distribution and the smallest number of species.

The proportions of four quantitative features (community species coverage, abundance, richness and biomass) in the functional groups of community with soil temperature and moisture changes are shown in Fig. 5B. The proportions of gramineae coverage, abundance, richness and biomass in the community all increased with soil temperature increasing. Besides, the proportions of perennial forb coverage, abundance, richness and biomass decreased with soil temperature increasing. With the soil moisture

increased, the proportions of gramineae coverage, abundance, richness and biomass all decreased. In contrast, the corresponding proportions of sedges, perennial forbs and annual forbs increased, and the most rapid rate of increase was found in perennial forbs.

The shift of dominant species in the community with soil temperature and moisture changes is shown in Fig. 5C. With the soil temperature increased, the plant community shifted as follows: *Polygonum viviparum* + *Kobresia capillifolia* → *Kobresia capillifolia* + *Artemisia phaeolepis* → *Kobresia humilis* + *Leymus secalinus* → *Leymus secalinus* + *Koeleria cristata* → *Leymus secalinus* + *Artemisia frigida*. With the soil moisture decreased, the plant community shifted as follows: *Polygonum viviparum* + *Artemisia phaeolepis* → *Kobresia capillifolia* + *Artemisia phaeolepis* → *Kobresia capillifolia* + *Koeleria cristata* → *Kobresia humilis* + *Leymus secalinus* → *Leymus secalinus* + *Koeleria cristata* → *Stipa krylovii* + *Leymus secalinus*. The integrated effects of increasing soil temperature and decreasing moisture on the plant community caused a shift from sedge-controlled to gramineae-controlled communities (Fig. 5C).

4. Discussion and conclusions

4.1. Potential to apply the mountain space-for-time substitution method to predict climate-related changes in a data-poor alpine ecosystem on the Tibetan Plateau

The changes rate of natural gradient in a hill is lower than the possible rates of change in species distributions and soil characteristics under climate change, resulting a good prediction throughout the slowly changing spatial gradients for long-term climate changing in the future

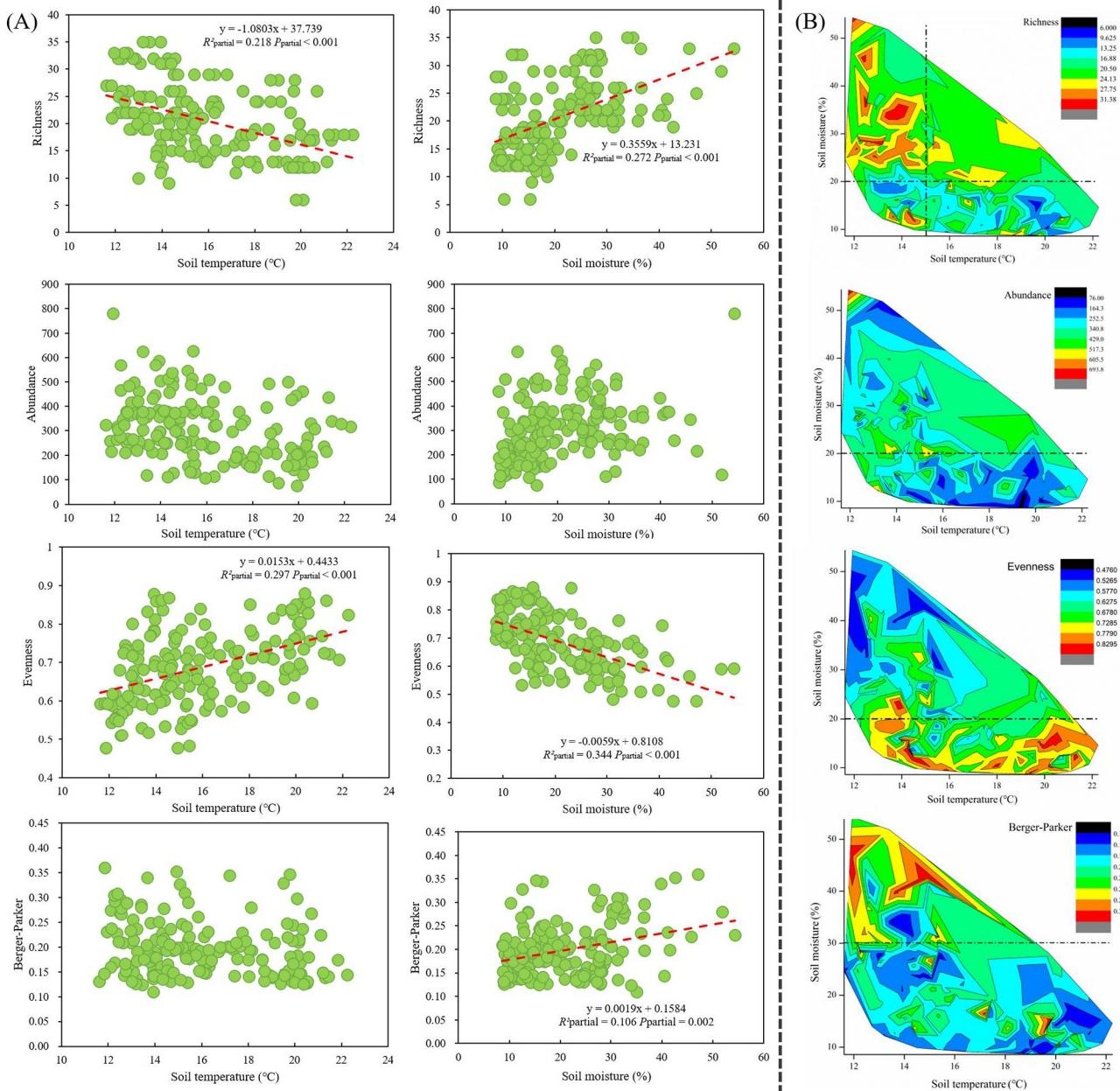


Fig. 3. Changes in the species diversity of the plant community under the individual (A) and integrated (B) effects of soil temperature and moisture.

(Cortés and Wheeler, 2018). This study predicts the potential climate-related changes of plant community in alpine meadow ecosystems based on a spatial gradient at hill scale with covering several hundred hectares. Although we had an alpine meadow as a case study, the method could be applied across a wide range of data-poor alpine rangeland ecosystem types, such as alpine steppe, alpine swamp, etc.

This demonstrated ability to transfer information and understanding from a well-studied mountain alpine ecosystem to another less-studied climate-related changes should lead to substantial improvement in the accuracy and utility of future predictions of ecological responses to climate change (Lester et al., 2014). In this case, a well-chosen mountain natural gradient that spans the range of likely future climate-related change enables quantitatively informed extrapolation of ecosystem response. Mountain can serve as surrogate to study climate-linked changes due to global change. Our study is based on deductive logic with pace-for-time substitution, although there is no real mountain replication. Oksanen (2001) summarized that if the experiment is based on deductive logic, the rules of the game are entirely different, the

replication is not an essential part of experimental design. Therefore, the results still had great value of application and prediction. From the view of generic relationships among all the plant community types, the method can predict climate-linked spatial or temporal succession from an original type to a new community type (Panetta et al., 2018). Hence, there is the potential to develop future scenarios for possible change in the community type in response to climate change (soil temperature and moisture gradients have been mainly used to describe climate change) in the coming year. The approach is also likely to be of substantial value even when reasonable data sets are available for the target domain, but climate change predictions lie outside the range of these data.

4.2. Plant diversity significantly decreases with climate warming in an alpine meadow on the Tibetan Plateau

Climate warming has become an incontrovertible fact. The IPCC (2007) has predicted that the temperature will increase by an average

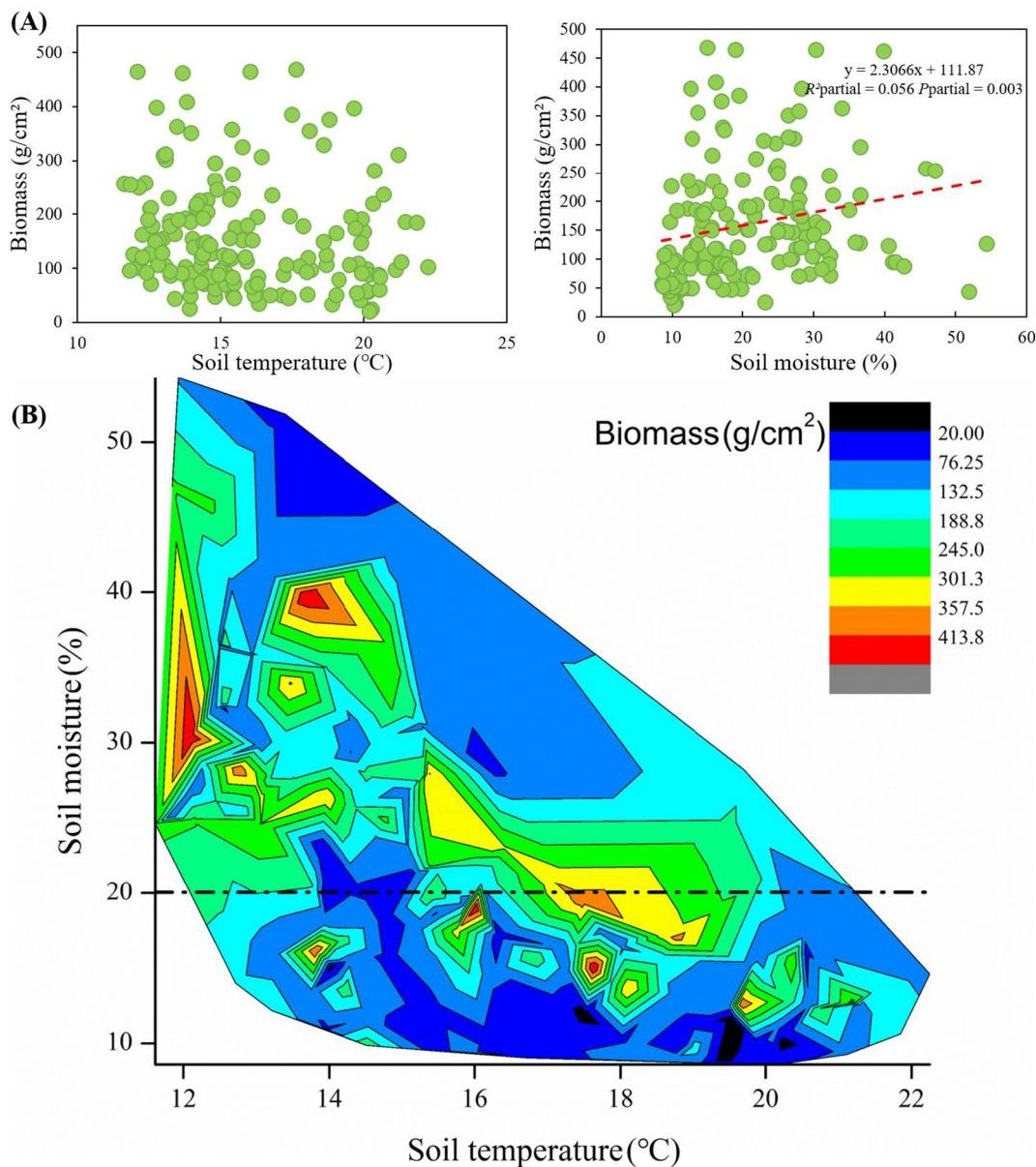


Fig. 4. The individual (A) and integrated (B) effects of soil temperature and moisture on biomass.

of 1.1–6.4 °C on the Earth's surface by the end of this century. Especially at high latitudes regions in the northern hemisphere. The Tibetan Plateau is a critical area of plant diversity that is sensitive to climate change, and plants in this alpine ecosystem are particularly sensitive to climate change (Ma et al., 2017). Climate change is one of the main threats to species diversity, and it may be strongly affected by climate warming (Sedlacek et al., 2014; Wheeler et al., 2015; Sedlacek et al., 2015). Climate warming has changed the species composition and community structure in alpine ecosystems and exerted both positive and negative effects on alpine plant diversity. On the one hand, the migration of low-altitude plants to high altitudes can increase the diversity of alpine plants (Steinbauer et al., 2018). Thüller et al. (2005) found that over the past 100 years, the migration of species from low altitudes has significantly increased plant diversity in the alpine zone in Switzerland. On the other hand, climate warming may also reduce plant diversity in the alpine zone, resulting in extinction or substitution of alpine plants or dominant species with other species due to the disappearance of suitable habitats (Sedlacek et al., 2015; Wheeler et al., 2016). Sommer et al. (2010) proposed that the average level of global plant diversity would drop by 9.4% in the most pessimistic model, with global warming of 4

°C and without any preventive measures against climate warming. In our study, at the quadrat scale, species richness decreased by 1.08 species for every 1 °C increase in soil temperature, and it decreased by 3.56 species for every 10% decrease in soil moisture (Fig. 3). Over the past 65 years, there has been an average temperature increase of 0.23 °C per decade in the study area, but no trend of significant changes was observed in the average annual precipitation, resulting in increasing soil temperature and a consequent decrease in soil moisture. The integrated effects of soil temperature increasing and moisture decreasing will lead to a rapid decrease in species richness. The community species abundance was not related to soil temperature or moisture at the quadrat scale; this indicates that for the species that disappeared in the alpine meadow with climate change, the community would compensate by increasing the abundances of existing species. Species evenness increased significantly with increasing soil temperature, and it decreased significantly with increasing soil moisture. At the quadrat scale, the niche space of community species decreased as soil temperature increased. In the limited niche space, the intensity of niche differentiation increased, the number of coexisting species decreased. Climate warming may lead to the loss and fragmentation of suitable plant

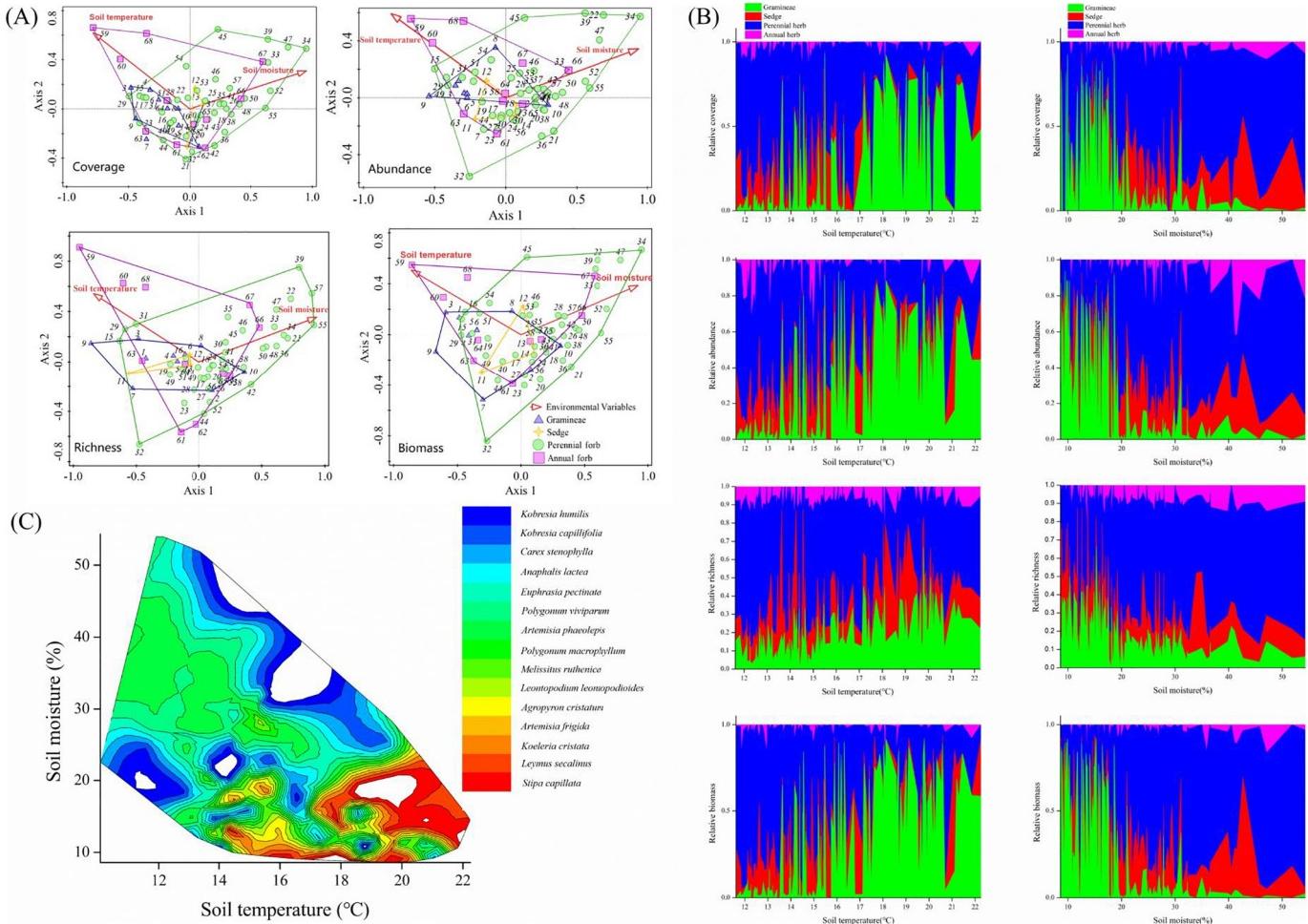


Fig. 5. The possible succession directions of the community under the individual and combined effects of soil temperature and moisture. A: Effects of soil temperature and moisture on the coverage, abundance, richness and biomass of the plant community in the unit of species (Scatter of classified case symbols (for plant functional groups) with members of individual species (represented by different numbers: 1–10, gramineae; 11–14, sedge; 15–57, perennial forb; 58–68, annual forb) enclosed in polygons). B: Response of functional groups in the plant community to soil temperature and moisture. C: Combined effects of soil temperature and moisture on the dominant species of the plant community.

habitats, the prediction of plant diversity change depends on whether there is sufficient time for the migration of alpine plants and for substitution between species. The diversity of species was affected by a combination of soil temperature and moisture; however, the interaction effects were complicated. Species richness was higher in low-temperature, high-moisture areas, whereas low-moisture areas had lower richness, lower community species abundance, higher evenness and lower dominance. This result indicates that, with the general trend of global climate warming, environmental factors such as precipitation should be taken into account in the prediction of plant diversity. This also indicates that under conditions of constant soil moisture, plant diversity is more easily affected by climate warming in the high-moisture area of the Tibetan Plateau.

4.3. Community biomass remains unchanged with climate warming but is strongly affected by species richness in an alpine meadow on the Tibetan Plateau

Climate change, especially warming, directly affects plant community biomass across a range of alpine ecosystems (Wheeler et al., 2015; Sedlacek et al., 2015). Climate warming can decrease the soil moisture to suppress plant growth or increase plant respiration to consume organic matter, thus reducing the biomass (Dai et al., 2009). Moreover, climate warming can promote the production of organic matter by enhancing plant photosynthesis or the uptake of mineral nutrients (Chen et al., 2017). Therefore, there are uncertainties in the

effects of temperature increase on plant biomass. Chen et al. (2017) conducted a 3-year simulation experiments of temperature increase in an alpine meadow on the Tibetan Plateau. They found that increasing temperature markedly increased the richness and biomass of gramineae and leguminosae, and the total biomass was also increased. However, other researchers found that vegetation markedly degenerated due to global climate warming, which resulted in varying degrees of decrease in the total biomass of alpine grasslands (Klein et al., 2007; Post and Pedersen, 2008). In our study, we found that the plant community biomass was not affected by temperature change and increased with soil moisture increasing. Plants have responded specifically to various temperature caused by different micro-environment during the long-term evolution process in alpine region and are able to effectively use solar energy for organic matter production under their respective temperature conditions. Besides, the biomass has a strong correlation with nutrient availability, microbial activity and other biotic influences, which are more important drivers of biomass in alpine meadows (Wheeler et al., 2014; Sedlacek et al., 2014; Little et al., 2016). Although, these factors were unmeasured in our study, it is well known that water is key factor for plant biomass in grasslands. Previous studies have also found that the productivity of alpine grasslands is highly responsive to rainfall, indicating the importance of water conditions in constraining alpine vegetation production (Shi et al., 2014; Liu et al., 2018). Further analysis also revealed that biomass production remained relatively low in low-moisture areas, regardless of soil temperature (Fig. 4). The appearance of two highest biomass under the conditions (soil

temperature 14 °C and moisture 40%; soil temperature 18 °C and moisture 20%) were exactly coincident with the two peaks of estimated richness under soil temperature and moisture (Supplementary Fig. 1). This result indicates a close relationship between biomass and species richness during climate change. There are three possible reasons for the high biomass under high diversity conditions (Chase and Leibold, 2002): (1) regions with higher average productivity may also have a larger degree of heterogeneity in environmental factors (including productivity itself), which could increase species dissimilarity. (2) regions with higher average productivity may also have a higher propensity for temporal variation in local species composition, which could increase species dissimilarity and (3) regions with higher average productivity may also have a higher propensity for temporal variation in local species composition, which could increase species dissimilarity.

4.4. The change of community composition with climate warming is more dependent on the migratory ability of broadleaf forbs

In the context of global climate change, changes in conditions such as water and heat are bound to break the interrelationships among plant species in the natural ecosystem after long-term adaptation and evolution (Little et al., 2016). This leads to changes in the species distribution pattern in the ecosystem and causes changes in the ecosystem structure and function. From the perspective of a single species, species migrate from the high-temperature area towards the low-temperature area under climate warming (Steinbauer et al., 2018). However, the response patterns of different plant functional groups to climate change are also different, and plants that have shorter life cycles and a higher frequency of species regeneration migrate faster (Wheeler et al., 2015). Cortés et al. (2014) also concluded that snowmelt differences resulted in phenological isolation but not in genetic differentiation in highly heterogeneous alpine environments. The effects of small-scale heterogeneity in snowmelt timing on the distribution of species are a concern that also needs to be addressed in future studies. The results of this study showed that under climate warming, the plant community shifted with the soil temperature increase as follows: *Polygonum*

viviparum + *Kobresia capillifolia* → *Kobresia capillifolia* + *Artemisia phaeolepis* → *Kobresia humilis* + *Leymus secalinus* → *Leymus secalinus* + *Koeleria cristata* → *Leymus secalinus* + *Artemisia frigida*. Sedges showed a concentrated distribution, whereas annual and perennial forbs were distributed in a broader range, and there were always suitable for broadleaf forbs that adapted well to changes of soil temperature and moisture. Different plant functional groups showed varying response patterns and sensitivities to climate warming. With soil temperature increased, the gramineae in the community increased, and the extent of the increase was the largest among the four functional groups. In contrast, the perennial forbs decreased, and the extent of decrease was the largest among the four functional groups (Fig. 5B). The changes of the functional groups with moisture also showed that gramineae and broadleaf forbs responded positively to environmental changes. Sedges were relatively stable, and the succession of plant community composition with climate warming was dependent on the migration ability of gramineae and perennial broadleaf forbs. However, the spatial distributions of long-lived, asexually propagated species, such as gramineae and sedge, are expected to lag behind rapid climatic changes, and their migration rates are slower than plants propagated by seeds and thus potentially make dispersal distances to new climatically suitable areas prohibitively large (Sedlacek et al., 2016). Hence, the migratory ability of broadleaf forbs dominated the change in community type with climate warming. Due to the limitation of low-temperature areas and migration barriers (ridges), the species competition is more intense because more species move to the low-temperature area (Fig. 6A), and environmental and (Alexander et al., 2017; Wason et al., 2017). When there is no route for the migration of species in the original high-temperature area (Fig. 6B), these species could only be replaced by species that are more resistant to high temperatures. Climate change will also result in competitive pressures on native plant species by migratory species, and less competitive native species are very likely to go extinct.

Our study clearly indicates that vegetation distribution along soil temperature and moisture gradients at hill scale can inform us the responses of plant communities to climate change on the scale of

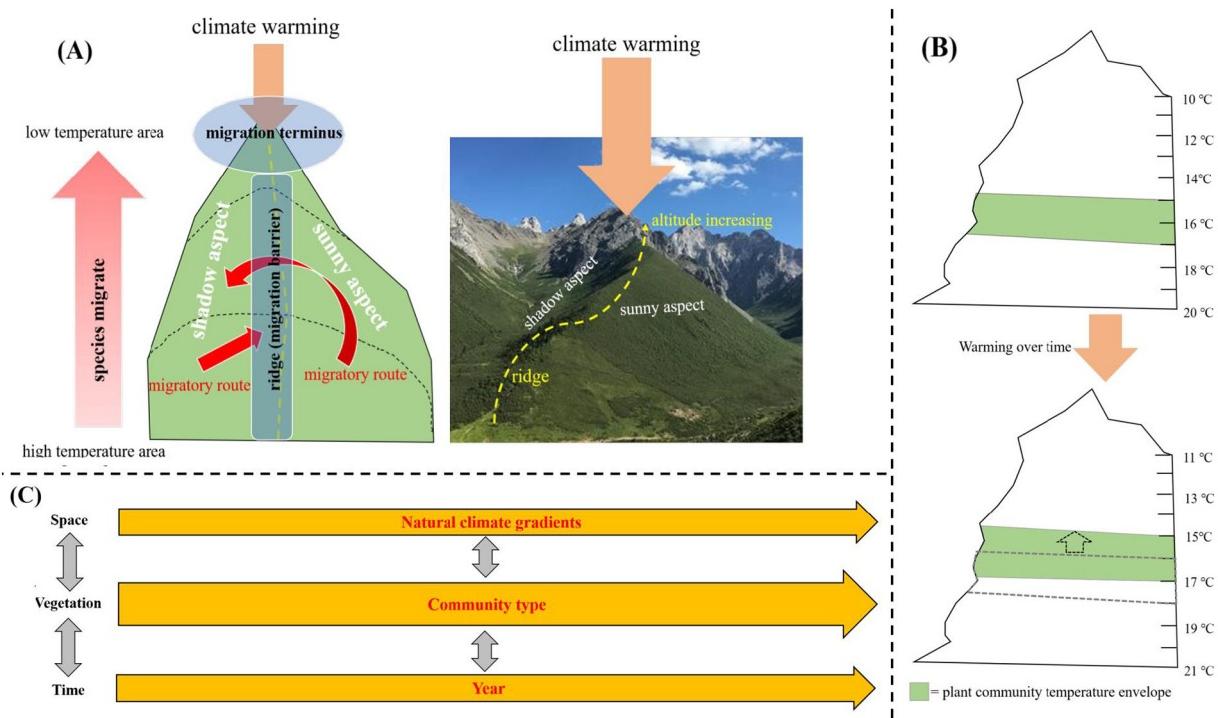


Fig. 6. A: The possible mountain species migratory route. B: A hypothetical temperature envelope on one mountain can shift upslope with climate warming. C: Natural gradient-vegetation distribution to examine the long-term patterns.

centuries. Future work should study the migration abilities of different species under climate warming on hill on the Tibetan Plateau. By integrating a long-term fixed climate studies, accompanied by equally long-term plant community censusing, with natural gradient-vegetation distribution on small-scale hill to examine the long-term community patterns (Fig. 6C), we can more accurately and effectively predict changes in plant community under climate changes in the alpine meadow on the Tibetan Plateau.

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References

- Alexander, J.M., Chalmandrier, L., Lenoir, J., Burgess, T.I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Martin, A., Nunez, M.A., Pauchard, A., Rabitsch, W., Rew, L.J., Sanders, N.J., Pellissier, L., 2017. Lags in the response of mountain plant communities to climate change. *Glob. Chang. Biol.* 24 (2), 563–579.
- Baldwin, A.H., Jensen, K., Schönenfeldt, M., 2014. Warming increases plant biomass and reduces diversity across continents, latitudes, and species migration scenarios in experimental wetland communities. *Glob. Chang. Biol.* 20, 835–850.
- Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T., Ferrier, S., 2013. Space can substitute for time in predicting climate-change effects on biodiversity. *Proc. Natl. Acad. Sci. U. S. A.* 110 (23), 9374–9379.
- Chase, J.M., Leibold, M.A., 2002. Spatial scale dictates the productivity-biodiversity relationship. *Nature* 416 (6879), 427–430.
- Chen, H., Zhu, Q., Peng, C., Wu, N., Wang, Y., Fang, X., Gao, Y., Zhu, D., Yang, G., Tian, J., Kang, X., Piao, S., Ouyang, H., Xiang, W., Luo, Z., Jiang, H., Song, X., Zhang, Y., Yu, G., Zhao, X., Gong, P., Yao, T., Wu, J., 2013. The impacts of climate change and human activities on biogeochemical cycles on the Qinghai-Tibetan plateau. *Glob. Chang. Biol.* 19 (10), 2940–2955.
- Chen, J., Luo, Y., Xia, J., Wilcox, K.R., Cao, J., Zhou, X., Jiang, L., Niu, S., Estera, K.Y., Huang, R., Wu, F., Hu, T., Liang, J., Shi, Z., Guo, J., Wang, R., 2017. Warming effects on ecosystem carbon fluxes are modulated by plant functional types. *Ecosystems* 20 (3), 515–526.
- Cortés, A.J., Wheeler, J.A., 2018. The environmental heterogeneity of mountains at a fine scale in a changing world. (pp.187–102). In: Hoorn, C., Perrigo, A., Antonelli, A. (Eds.), *Mountains Climate and Biodiversity*. Wiley Blackwell, Hoboken.
- Cortés, A.J., Waeber, S., Lexer, C., Sedlacek, J., Wheeler, J.A., Van, K.M., Bossdorf, O., Hoch, G., Rixen, C., Wipf, S., Karrenberg, S., 2014. Small-scale patterns in snowmelt timing affect gene flow and the distribution of genetic diversity in the alpine dwarf shrub *Salix herbacea*. *Heredity* 113 (3), 233–239.
- Dai, A., Trenberth, K.E., Qian, T., 2009. A global data set of palmer drought severity index for 1870–2002: relationship with soil moisture and effects of surface warming. *J. Hydrometeorol.* 5 (6), 1117–1130.
- Dunne, J.A., Saleska, S.R., Fischer, M.L., Harte, J., 2004. Integrating experimental and gradient methods in ecological climate change research. *Ecology* 85 (4), 904–916.
- Garcia, R.A., Cabeza, M., Rahbek, C., Araújo, M.B., 2014. Multiple dimensions of climate change and their implications for biodiversity. *Science* 344, 1247579.
- Harte, J., Saleska, S.R., Levy, C., 2015. Convergent ecosystem responses to 23-year ambient and manipulated warming link advancing snowmelt and shrub encroachment to transient and long-term climate-soil carbon feedback. *Glob. Chang. Biol.* 21, 2349–2356.
- IPCC Climate Change, 2007. The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.
- Klein, J.A., Harte, J., Zhao, X.Q., 2007. Experimental warming, not grazing, decreases rangeland quality on the Tibetan plateau. *Ecol. Appl.* 17, 541–557.
- Lester, R.E., Close, P.G., Barton, J.L., Pope, A.J., Brown, S.C., 2014. Predicting the likely response of data-poor ecosystems to climate change using space-for-time substitution across domains. *Glob. Chang. Biol.* 20, 3471–3481.
- Little, C.J., Wheeler, J.A., Sedlacek, J., Cortés, A.J., Rixen, C., 2016. Small-scale drivers: the importance of nutrient availability and snowmelt timing on performance of the alpine shrub *Salix herbacea*. *Oecologia* 180 (4), 1015–1024.
- Liu, H.Y., Mi, Z.R., Lin, L., Wang, Y.H., Zhang, Z.H., Zhang, F.W., Wang, H., Liu, L.L., Zhu, B., Cao, G.M., Zhao, X.Q., Sanders, N.J., Classen, A.T., Reich, P.B., He, J.S., 2018. Shifting plant species composition in response to climate change stabilizes grassland primary production. *Proc. Natl. Acad. Sci.* 115, 4051–4056.
- Ma, Z., Liu, H., Mi, Z., Zhang, Z., Wang, Y., Wei, X., Jiang, L., He, J., 2017. Climate warming reduces the temporal stability of plant community biomass production. *Nat. Commun.* 8 (8), 15378.
- Madriñán, S., Cortés, A.J., Richardson, J.E., 2013. Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Front. Genet.* 4 (4), 192.
- Magurran, A.E., 1988. *Ecological Diversity and its Measurement*. Springer, New York.
- Oksanen, L., 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos* 94 (1), 27–38.
- Panetta, A.M., Stanton, M.L., Harte, J., 2018. Climate warming drives local extinction: evidence from observation and experimentation. *Sci. Adv.* 4, eaao1819.
- Post, E., Pedersen, C., 2008. Opposing plant community responses to warming with and without forbivores. *Proc. Natl. Acad. Sci. U. S. A.* 105, 12353–12358.
- Rudgers, J.A., Kivlin, S.N., Whitney, K.D., Price, M.V., Waser, N.M., Harte, J., 2014. Responses of high-altitude graminoids and soil fungi to 20 years of experimental warming. *Ecolgy* 95, 1918–1928.
- Seddon, A.W., Maciasfaura, M., Long, P.R., Benz, D., Willis, K.J., 2016. Sensitivity of global terrestrial ecosystems to climate variability. *Nature* 531, 229–232.
- Sedlacek, J.F., Bossdorf, O., Cortés, A.J., Wheeler, J.A., Kleunen, M.V., 2014. What role do plant-soil interactions play in the habitat suitability and potential range expansion of the alpine dwarf shrub *Salix herbacea*? *Basic Appl. Ecol.* 15 (4), 305–315.
- Sedlacek, J., Wheeler, J.A., Cortés, A.J., Bossdorf, O., Hoch, G., Lexer, C., Wipf, J., Karrenberg, S., Kleunen, M.V., Rixen, C., 2015. The response of the alpine dwarf shrub *Salix herbacea* to altered snowmelt timing: lessons from a multi-site transplant experiment. *PLoS One* 10 (4), e0122395.
- Sedlacek, J., Cortés, A.J., Wheeler, J., Bossdorf, O., Hoch, G., Klápková, J., Lexer, C., Rixen, C., Wipf, S., Karrenberg, S., Kleunen, M., 2016. Evolutionary potential in the Alpine: trait heritabilities and performance variation of the dwarf willow *Salix herbacea* from different elevations and microhabitats. *Ecol. Evol.* 6, 3940–3952.
- Shen, M., Piao, S., Dorji, T., Liu, Q., Cong, N., Chen, X., An, S., Wan, S., Wang, T., Zhang, G., 2015. Plant phenological responses to climate change on the Tibetan Plateau: research status and challenges. *Nat. Sci. Rev.* 2, 454–467.
- Shi, Y., Wang, Y., Ma, Y., Ma, W., Liang, C., Flynn, D.F.B., Schmid, B., Fang, J.Y., He, J.S., 2014. Field-based observations of regional-scale, temporal variation in net primary production in Tibetan alpine grasslands. *Biogeosciences* 11 (7), 16843–16878.
- Šmilauer, P., Lepš, J., 2014. *Multivariate Analysis of Ecological Data Using Canoco 5*. Cambridge University Press, Cambridge.
- Sommer, J.H., Kretz, H., Kier, G., Jetz, W., Mutke, J., Barthlott, W., 2010. Projected impacts of climate change on regional capacities for global plant species richness. *Proc. R. Soc. B Biol. Sci.* 277, 2271–2280.
- Steinbauer, M.J., Grytnes, J.A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchalter, M., Barni, E., Bjorkman, A.D., Breiner, F.T., Burg, S., Czortek, P., Dawes, M.A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V.A., Fernández-Arberas, O., Fossheim, K.F., Gómez-García, D., Georges, D., Grindrud, E.T., Haider, S., Haugum, S.V., Henriksen, H., Herreros, M.J., Jaroszewicz, B., Jaroszynska, F., Kanka, R., Kapfer, J., Klanderud, K., Kühn, I., Lamprecht, A., Matteo, M., Morra di Celli, U., Normand, S., Odland, A., Olsen, S.L., Palacio, S., Petey, M., Piscová, V., Sedlakova, B., Steinbauer, K., Stöckli, V., Svensson, J.-C., Teppa, C., Theurillat, J.-P., Vittoz, P., Woodin, S.J., Zimmerman, N.E., Wipf, S., 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* 556, 231–234.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., Mooney, H.A., 2005. Climate change threats to plant diversity in Europe. *Proc. Natl. Acad. Sci. U. S. A.* 102, 8245–8250.
- Travis, S., Hester, M., 2005. A space-for-time substitution reveals the long-term decline in genotypic diversity of a widespread salt marsh plant, *Spartina alterniflora*, over a span of 1500 years. *J. Ecol.* 93 (2), 417–430.
- Wang, S., Duan, J., Xu, G., Wang, Y., Zhang, Z., Rui, Y., Luo, C., Xu, B., Zhu, X., Chang, X., Cui, X., Niu, H., Zhao, X., Wang, W., 2012. Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow. *Ecology* 93 (11), 2365–2376.
- Wason, J.W., Bevilacqua, E., Dovciak, M., 2017. Climates on the move: implications of climate warming for species distributions in mountains of the northeastern United States. *Agric. For. Meteorol.* 246, 272–280.
- Wheeler, J.A., Hoch, G., Cortés, A.J., Sedlacek, J., Wipf, S., Rixen, C., 2014. Increased spring freezing vulnerability for alpine shrubs under early snowmelt. *Oecologia* 175 (1), 219–229.
- Wheeler, J.A., Schnider, F., Sedlacek, J., Cortés, A.J., Wipf, S., Hoch, G., Rixen, C., 2015. With a little help from my friends: community facilitation increases performance in the dwarf shrub *Salix herbacea*. *Basic Appl. Ecol.* 16 (3), 202–209.
- Wheeler, J.A., Cortés, A.J., Sedlacek, J., Karrenberg, S., Kleunen, M., Wipf, S., Hoch, G., Bossdorf, O., Rixen, C., 2016. The snow and the willows: earlier spring snowmelt reduces performance in the low-lying alpine shrub *Salix herbacea*. *J. Ecol.* 104 (4), 1041–1050.
- Yang, H., Wu, M., Liu, W., Zhang, Z., Zhang, N., Wan, S., 2011. Community structure and composition in response to climate change in a temperate steppe. *Glob. Chang. Biol.* 17, 452–465.